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Research Article

On the path to cosmopolitanism: the continuing geographic expansion of *Caprella mutica* (Crustacea, Amphipoda)

Jan Beermann[1], Marcelo M. Rivadeneira[2,3,4], Martin Thiel[3,4,5]

1 *Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Benthic Ecology, Am Handelshafen 12, 27570 Bremerhaven, Germany*
2 *Laboratory of Paleobiology, Center for Advanced Studies in Arid Zones (CEAZA), Coquimbo, Chile*
3 *Dpto. de Biología Marina, Facultad Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile*
4 *Center of Ecology and Sustainable Management of Oceanic Island (ESMOI), Coquimbo, Chile*
5 *MarineGEO Program, Smithsonian Environmental Research Center, Edgewater, Maryland, USA*
Corresponding author: Jan Beermann (jan.beermann@awi.de)

Abstract

Human activities have been transporting caprellid amphipods (or "skeleton shrimps") across the oceans for many decades. As a result, some caprellid amphipods now are among the most widespread non-indigenous species in many different coastal regions of the world. The global spread of these species is still ongoing in some cases, such as that of the successful invader *Caprella mutica* Schurin, 1935. Here, we report on the arrival of *C. mutica* in South America and modelled its environmental niche based on its current global distribution in order to evaluate future expansion risks. The species distribution model confirmed high occupancy probabilities for already invaded areas of Europe and North America with generally lower probabilities in the southern hemisphere and mean sea surface temperature as best predictor. Further, the model suggested that our discovery of *C. mutica* in northern Chile was made in a region that is less favorable for this species, while occupancy probabilities increased further south. Given the invasion history of *C. mutica* in other marine regions of the world and the more favorable oceanographic conditions, a further spread of this invader southwards along the South American Pacific coast seems very likely.

Key words: Biofouling, biological invasion, marine dispersal, marine shipping, non-indigenous species

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Introduction

Many marine species have been transported by human activities across the oceans to other coastal regions where they established as non-indigenous species (NIS). This human-mediated spread creates recent 'neocosmopolitan' distributions of species (i.e. extensive geographical ranges through anthropogenic dispersal) among coastal benthic habitats around the world (Darling and Carlton 2018). Crustaceans, including barnacles, shrimps, crabs and peracarids are among some of the most ubiquitous NIS worldwide (Ruiz et al. 2011; Bailey et al. 2020). While large decapod species have likely been transported in ballast water of cargo ships (Rodríguez and Suárez 2001), many smaller amphipod species are assumed to have been dispersed as stowaways on ship hulls or with aquaculture activities (e.g. Marchini and Cardeccia 2017; Albano and Obenat 2019; Martínez-Laiz et al. 2019; Guerra-García et al. 2023). Many of these amphipod NIS are now cosmopolitan species

but their former native ranges cannot always be determined (Beermann et al. 2020; Martínez-Laiz et al. 2021). This is because their invasion history is often ancient, sometimes dating back hundreds of years to the first circumglobal expeditions (Darling and Carlton 2018; Beermann et al. 2020).

Interestingly, caprellid amphipods are among the most widespread neocosmopolitan species that have become NIS in many different regions of the world (Cabezas et al. 2010; Ros et al. 2016; Marchini and Cardeccia 2017; Martínez-Laiz et al. 2021). For example, *Caprella scaura* Templeton, 1836 successfully established dense populations all around the globe in warm-temperate to tropical waters where it thrives in fouling communities on man-made substrata (e.g. Guerra-García et al. 2011; Martínez-Laiz et al. 2021). At least in southern Europe, it competes with another cosmopolitan caprellid, *Caprella equilibra* Say, 1918, which can occur in the same habitats (Foster et al. 2004; Ros et al. 2015; Marchini and Cardeccia 2017).

In recent decades, many new species introductions had been recognized shortly after their initial arrival in new regions. The invasion history of these newly introduced species could be documented, allowing to better understand the mechanisms of transport and expansion into new regions. One of these cases of ongoing invasions is the caprellid amphipod *Caprella mutica* Schurin, 1935. Native to North-East Asia, it was described from the Sea of Japan (Schurin 1935; Vassilenko 1967; Arimoto 1976) before it established populations on many coasts outside its native range within a relatively short time (Boos et al. 2011; Marchini and Cardeccia 2017). The successful establishment of amphipod NIS in an area can result in a displacement of ecologically similar native species (e.g. Dick 1996; Dick et al. 1999). Correspondingly, mass occurrences of invasive *C. mutica* have been linked to a scarcity of native caprellids in the same habitats such as *Caprella linearis* (Linnaeus, 1767) in the North East Atlantic (e.g. Coolen et al. 2016). This could be due to direct interference competition between the invader and native caprellids (Shucksmith et al. 2009) although differential habitat demands (Coolen et al. 2016) may facilitate a spatial segregation and thus resource partitioning (Schoener 1986). Based on its known habitat preferences and environmental tolerances, Boos et al. (2011) speculated on a future range expansion of *C. mutica* to several coastlines around the globe where it had not been reported yet, but environmental conditions seemed favorable. Among these potentially vulnerable regions were the Pacific and Atlantic coasts of South America.

In South America, only few amphipod NIS have been reported so far, and they are often underrepresented or even completely absent from NIS inventories (e.g. Ferreira et al. 2009; Cárdenas-Calle et al. 2019; Carlton et al. 2019; Teixeira and Creed 2020; Zambrano and Ramos 2021; Rodríguez-Gavilanes et al. 2024), or their status is not well known and many species are categorized as cryptogenic (e.g. Orensanz et al. 2002). An exception to this general pattern is the Argentinian coast, where 18 amphipod NIS (including introduced and cryptogenic species) have been reported, among them three caprellid species (Schwindt et al. 2020). The cosmopolitan species *Caprella danilevskii* Czerniavsky, 1868, *C. equilibra* and *C. scaura* have been reported widely from the Atlantic and Pacific coasts of South America (Guerra-García and Thiel 2001; Díaz et al. 2005; Cunha et al. 2018; Chunga-Llauce et al. 2023b). Furthermore, the caprellid *Paracaprella pusilla* Mayer, 1890 also has recently been reported as NIS from locations along the Pacific coast (Alarcón-Ortega et al. 2015; Ros et al. 2016; Alfaro-Montoya and Ramírez Alvarado 2018; Chunga-Llauce et al. 2022), suggesting that caprellid invasions might not go entirely undetected along the coasts of South America.

Few amphipod NIS have been reported for the coasts of Chile. In their review of marine NIS of the southeastern Pacific, Castilla and Neill (2009) listed no amphipod NIS for the coasts of Chile and Peru. However, two frequently occurring species of the genus *Jassa* Leach, 1814 have been confirmed to be NIS in Chile and South America in general (Beermann et al. 2020). Further, the cosmopolitan *Monocorophium acherusicum* (A. Costa, 1853) has been recorded from fouling communities in Chile (Pérez-Schultheiss 2009; Thiel and Hinojosa 2009), and several other amphipod species have been suggested as NIS for Chile (Marchini and Cardeccia 2017). The littoral caprellid fauna of Chile has been relatively well-characterized, based on extensive sampling in benthic and artificial habitats at 30°S in Coquimbo in northern central Chile (Guerra-García and Thiel 2001). A follow-up study then surveyed caprellids from harbor and aquaculture buoys along the Chilean coast between 18°S and 41°S, confirming the same species as previously reported for Coquimbo with the exception of the species *Deutella venenosa* Mayer, 1890, which seemed to be restricted to Coquimbo (Thiel et al. 2003). Since then, the caprellid fauna of Chile and Coquimbo in particular has been screened occasionally, also checking for potential newcomers (Astudillo et al. 2009; Rech et al. 2023).

The aim of this study is to (i) report the arrival of the successful invader *Caprella mutica* in South America, (ii) compile recent surveys of the caprellid fauna from several regions in South America, (iii) synthesize information about the current distribution of *Caprella mutica*, and (iv) build a species distribution model of *Caprella mutica* to evaluate the future expansion risk of this species along the South American coasts.

Material and methods

Sampling

Caprellid specimens were repeatedly collected at the same site with fouling assemblages from floating docks and on mooring lines of the aquaculture concessions of the Universidad Católica del Norte (UCN) in Bahía La Herradura in Coquimbo, Chile (29°57'58.4"S, 71°21'12.9"W) on August 30th, 31st and September 9th 2022. Several culture lines for scallop aquaculture are established in the concession of UCN, where lantern-nets are suspended from longlines (Bakit et al. 2024). These artificial structures host extensive fouling communities (Dumont et al. 2009) providing habitat to many mobile organisms (including several species of caprellid amphipods) (Astudillo et al. 2009). For the sampling procedure, the buoys and longlines were lifted up from a boat, and the fouling biomass was scraped from these artificial substrata and brought to the lab (approx. transport time: 10 min). For each sampling we collected an approximate volume of about 10 l fouling biomass, which included seaweeds, hydrozoans, bryozoans, tunicates, mussels and other sessile organisms (for species inventory see e.g. Astudillo et al. 2009). Additional material was obtained from samples collected the same way and at the same site on 23 June and 7 July 2023.

In the laboratory, the fouling organisms were immediately placed in large trays (approximately 20 cm x 30 cm surface area) with seawater, and the material was sorted alive. No signs of predation in the samples were observed during the procedure. All amphipods were retrieved and carefully inspected under a dissecting microscope. Caprellid amphipods were identified to the lowest taxonomic level, and counted. Voucher material was fixated in ethanol and deposited in the collection of the UCN.

During the years 2004 to 2023, caprellid amphipods were collected annually for the Invertebrate Zoology laboratories in the Marine Biology program of the Marine Science Faculty in Coquimbo (30°S). For these courses, usually a few hundred live caprellid individuals were brought to the teaching laboratory (on seaweeds, bryozoans and hydrozoans). The collection of caprellid amphipods was conducted in a very similar way as described above by sampling extensive amounts of fouling organisms with the associated caprellid amphipods. The samples were collected a few hours before the course, transported to the nearby lab, and maintained alive for students to observe and document the morphology and behavior of the caprellids. Students quantified the ventilation movements of ovigerous caprellid females and had to identify the particular species for which they recorded these behaviors using Guerra-García and Thiel (2001); the species identifications were usually checked by the course instructors.

Review of caprellid studies

In order to characterize the recent survey efforts focusing on the caprellid fauna in Central and South America, we searched the literature using the Web of Science and GoogleScholar. The keywords "Caprella" and "amphipod" were linked with the names of all Central and South American countries. In order to identify additional studies, all studies on caprellids that were published after 2000 were carefully examined for cross-citations. The recovered references were then scanned to identify those that reported on caprellid surveys in their regions or countries. These studies typically included species inventories that were based on targeted samplings of the caprellid fauna. All studies were conducted by invertebrate zoologists, often including amphipod or even caprellid specialists, who were very familiar with the taxonomic literature and species identifications. The investigations focused on shallow habitats up to approximately 20 m water depth, including fouling communities (e.g. Nunez Velazquez et al. 2017; Chunga-Llauce and Pacheco 2021; Chunga-Llauce et al. 2022) and macrophyte or animal reefs (Díaz et al. 2005; Alarcón-Ortega et al. 2017; Cunha et al. 2018). Usually the authors sampled several sites within their study region, where individual sites had distances of a few to > 100 km between them. Most studies covered one or maximally two ecoregions (*sensu* Spalding et al. 2007). References that focused only on the population or reproductive biology of selected caprellid species were not included.

For comparative purposes, we extracted presence/absence data from each respective study, which is common practice in biodiversity reviews of specific groups or regions (see e.g. Gallardo and Penchaszadeh 2001; Cárdenas-Calle et al. 2020; Durand et al. 2024). Only records on species-level were considered in the current data consolidation. The similar approaches used by all examined studies allowed for direct comparison in the context of the current overview.

Species distribution model (SDM) of *Caprella mutica*

Worldwide georeferenced occurrences for *C. mutica* were downloaded and curated from the Global Biodiversity Information Facility (GBIF, www.gbif.org; downloaded on 06 September 2023). The database was augmented by an exhaustive literature search and further published records were added (i.e. derived from:

Schurin 1935; Vassilenko 1967; Arimoto 1976; Locke et al. 2007; Ashton et al. 2008a; 2008b; Willis et al. 2009; Hosono 2011; Almón et al. 2014; Collin and Johnson 2014; Coolen et al. 2016; Peters and Robinson 2017; Heo et al. 2020; Lavrador et al. 2024). A total of 1388 occurrences of *C. mutica* were used for the model (excluding the current presence in Chile reported here; Fig. 1). The occurrences were thinned to reduce sampling biases (Aiello-Lammens et al. 2015), leaving only one presence per grid cell (0.08°, see below), resulting in 800 occurrences. We also compiled information on documented absences from sampled localities in South America (n = 170), where previous community-level studies of Caprellidae did not detect any specimens of *C. mutica*. While these absences were not used in the SDM, they were used to cross-validate the output of the SDM.

We used 13 oceanographic variables (Table 2) from the BioOracle database v.2.2. (Assis et al. 2018), with a 0.08° (~9.2 km^2) resolution. These variables have commonly been used by previous studies and covered a wide range of biophysical and geochemical conditions in the ocean (Bosch et al. 2018), also reflecting relevant ecophysiological stressors for *C. mutica* as proven by experimental studies (Cook et al. 2007; Lim and Harley 2018). Rasters were masked to include only coastal grid cells, as the species is restricted to shallow waters. The degree of collinearity of environmental predictors was examined by using a variance inflation factor (VIF) analysis where values of VIF > 10 have traditionally been used to claim high collinearity. VIF analyses were carried out using the library 'usdm' (Naimi et al. 2014) in R (ver. 4.1.0; R Core Team 2024). Two variables (mean and range of phytoplankton concentration) showed a high degree of collinearity and were removed from further analyses.

The SDM was built using recommended methodological protocols (Bosch et al. 2018; Feng et al. 2019; Zurell et al. 2020). We created 10,000 random pseudo-absences obtained from all coastal grid cells. We used a Maxent modeling approach, a

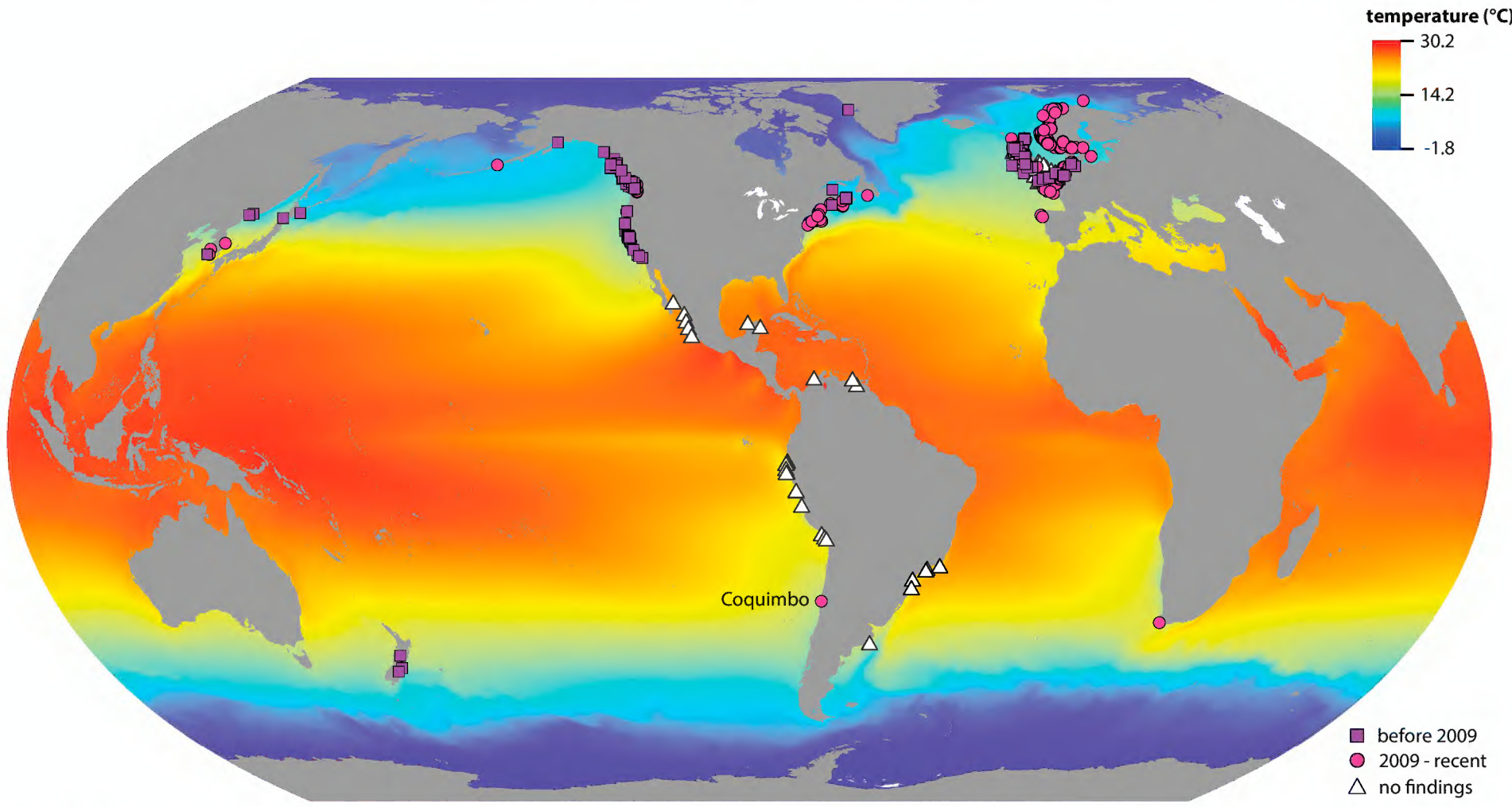

Figure 1. World oceans with mean sea surface temperature (SST) and confirmed reported presences and absences of *Caprella mutica* before and after the year 2009 (i.e. the survey of Boos et al. 2011) considered for this study. 'No findings' refers to sites where previous surveys had examined the caprellid fauna (see also Table 1) without finding *Caprella mutica*.

robust machine-learning algorithm successfully applied to implement SDMs (Elith et al. 2011; Phillips et al. 2017). The model fit was evaluated using the Area Under the Curve (AUC) of the Receiver Operating Characteristic Curve, where values close to 1 indicate a perfect fit. Analyses were conducted using the library 'SDMtune' (Vignali et al. 2020). The model's accuracy was maximized by hyper-parameter tuning and different combinations of the regularization parameter and feature classes. We used a genetic algorithm to assess 150 possible combinations of parameters, evaluating 15 populations in two generations. Genetic algorithms are computational optimization techniques inspired by the process of natural selection (Goldberg and Holland 1988; Alhijawi and Awajan 2024), enhancing model performance, selecting relevant variables, or optimizing parameters when predicting species distributions based on environmental data (Vignali et al. 2020). To ensure the robust spatial transferability of SDMs, we used a four-fold spatial cross-validation scheme based on a checkerboard pattern, implemented in the library ENMeval (Kass et al. 2021) in R. We evaluated the importance of all oceanographic variables in terms of percent contribution and permutation importance and estimated the functional relationship between the occupancy probability and the top predictors using partial dependence plots to isolate the effect of each predictor. A Multivariate Environmental Similarity Surfaces (MESS) analysis was carried out to evaluate areas with non-analog oceanographic conditions. MESS analyses were carried out using the library 'predicts' (Hijmans 2024) in R. Finally, we projected the probability of species occurrence onto the global coasts using ArcGIS Pro (ver. 3.3.0; ESRI Inc.).

Results

Caprella mutica in Coquimbo, Chile and its morphological distinction

In total, seven individuals of *C. mutica* (6 adult males and 1 ovigerous female) were found on August 30th, 31st and September 9th 2022. Besides this newly recorded NIS for this area, the 4 caprellid species *Caprella equilibra*, *Caprella verrucosa* Boeck, 1871, *Caprella scaura* and *Deutella venenosa* as well as the ischyrocerids *Jassa marmorata* Holmes, 1905, *Jassa slatteryi* Conlan, 1990 and *Ericthonius* cf. *rubricornis* (Stimpson, 1853), the maerid *Elasmopus rapax* A. Costa, 1853 (*sensu* Hughes and Lowry 2010), the aorid *Aora typica* Krøyer, 1845, the dexaminid *Paradexamine* cf. *pacifica* (Thomson, 1879) and a stenothoid *Stenothoe* sp. were found coexisting in the amphipod fouling communities of Bahía La Herradura.

In the course of the Marine Biology program of the Marine Science Faculty in Coquimbo, the dominant species in the samples varied between the years, but the most common species were *Caprella equilibra*, *C. scaura* and *C. verrucosa*, and on rare occasions *Deutella venenosa*; the species identified by the students (using Guerra-García and Thiel 2001) were frequently verified by one of the authors (MT). Prior to 2023, no *Caprella mutica* were found, but on 23 June 2023 a few caprellid amphipods examined by the students did not match any of the species reported in Guerra García and Thiel (2001). After closer examination, these individuals were confirmed to belong to *C. mutica*. In addition, two weeks later (7 July 2023), several individuals (adult males and females) of *C. mutica* were collected during a workshop on marine invasive species. The collected individuals have been deposited in the Biological Collection of the UCN (SCBUCN-5533 1 female + 1 male adult; SCBUCN-5537 1 female + 4 male adults; SCBUCN-5561 5 male adults).

The specimens of *Caprella mutica* collected in Coquimbo could be easily distinguished from its two sympatric congeners *C. verrucosa* and *C. scaura* by the absence of a projection on the head. Further, the individuals of *C. mutica* were characterized by numerous spiny projections on the dorsal surface of the pereonites (pereonites 1–7 in females, 3–7 in males), which distinguished them clearly from co-occurring *Caprella equilibra* (Fig. 2). In addition, hyperadult males exhibited dense setation on pereonites 1 and 2, and on gnathopod 2, leading to a conspicuous 'hairy' appearance, which is unique among the known *Caprella* species of the world (Platvoet et al. 1995 as '*Caprella macho*'; Guerra-García and Thiel 2001; Beermann and Franke 2011; Boos et al. 2011; Daneliya and Laakkonen 2012; Heo et al. 2020).

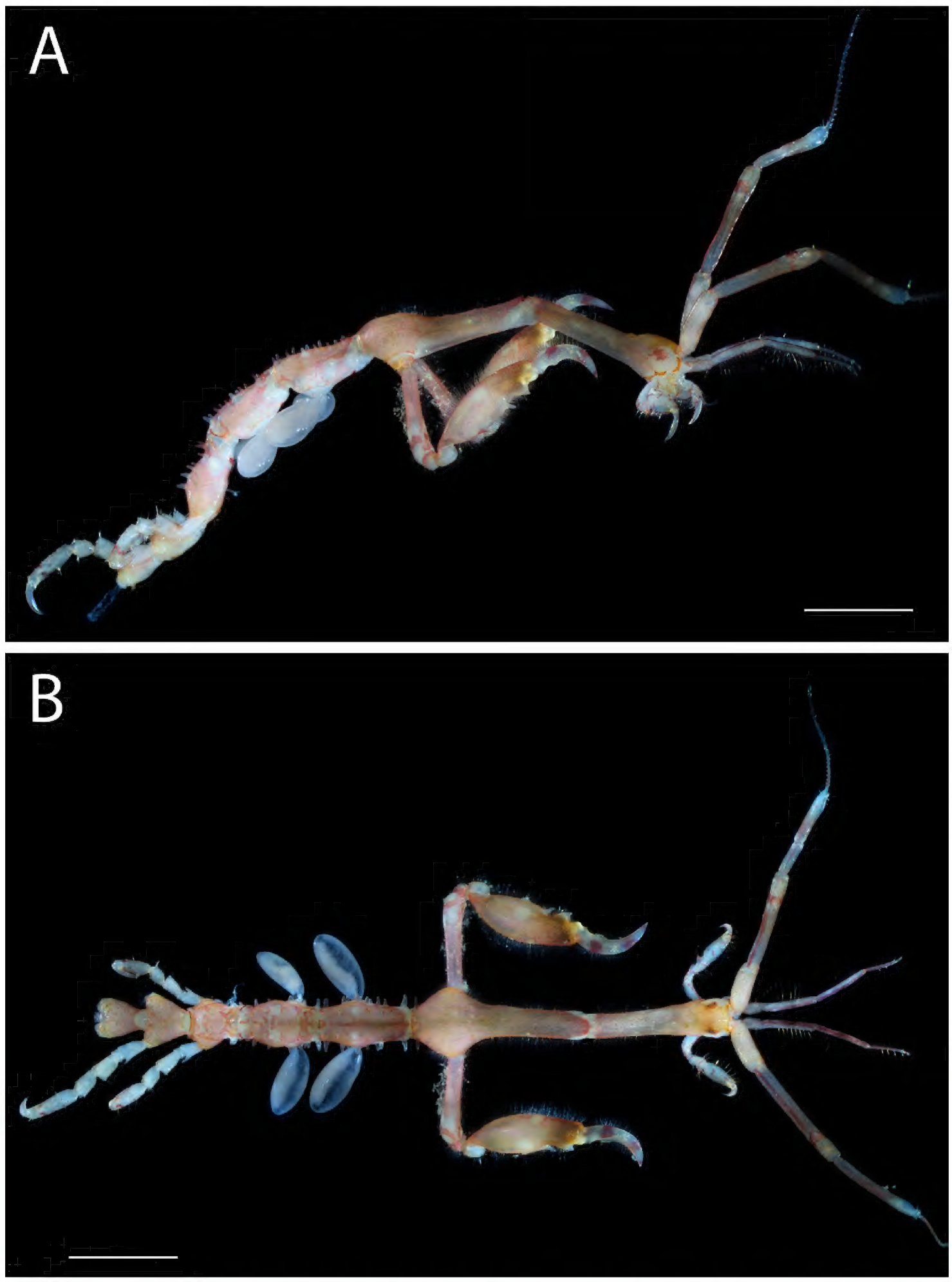

Figure 2. Individual of *Caprella mutica*, collected in Bahía La Herradura (Coquimbo, Chile) on 09 September 2022. Habitus of adult male **A** lateral view **B** dorsal view. Scale bars: 5 mm.

The Asian species *Caprella acanthogaster* Mayer, 1890 shares some morphological characteristics with *C. mutica* that may cause confusion, such as the dorsal spination on the pereonites and the hairy appearance of adult males (Faasse 2005; Daneliya and Laakkonen 2012; Heo et al. 2020). However, the specimens of *C. mutica* found in Bahía La Herradura were characterized by a dense hairy setation all over pereonites 1, 2 and gnathopod 2, whereas the hairy setation in *C. acanthogaster* is restricted to gnathopod 2 only. Further, *C. acanthogaster* bears a pair of two tiny tubercles on the head whereas *C. mutica* specimens from Chile had no tubercles or projections on the head.

Recent caprellid surveys in Central and South America

Over the course of the past 20–30 years, several surveys of the local caprellid fauna had been conducted in several countries of Central and South America (Table 1). These surveys documented a total of 25 caprellid species (of 27 taxa in total) on the Atlantic coast (between 21°N and 38°S), and 16 (of 17 taxa in total) species on the Pacific coast (between 23°N and 30°S). Only four of those species (*Caprella equilibra*, *C. penantis*, *C. scaura* and *Paracaprella pusilla*) were recorded on both Atlantic and Pacific coasts. No findings of *Caprella mutica* were reported in any of these surveys.

Following the initial survey of the local caprellid fauna by Guerra-García and Thiel (2001) and Thiel et al. (2003), the biota growing on aquaculture buoys in the Coquimbo region were again sampled and examined in 2007/08, and all previously identified caprellid species were recorded, but no *C. mutica* was found in that survey (Astudillo et al. 2009).

Species distribution model of *Caprella mutica* and risk of range expansion

The SDM exhibited a high accuracy (AUC = 0.96), and the MESS analyses showed that the model could be extrapolated to ~96% of the coastal grid cells. The model predicted a high probability of occupancy around the native area in Northeastern Asia, and the already invaded areas in Europe and North America (Fig. 3). In general, there was a lower probability of occupancy in the southern hemisphere, except for some areas in South Africa, South Australia, New Zealand, and Chile. Areas with confirmed absences were characterized by low occupancy probabilities (Fig. 3). Along the Chilean coast, the model predicted elevated probabilities (0.30–0.68) of occupancy between 32–42°S, which is 200 to 1,400 km south of the newly confirmed occurrence in the Coquimbo area reported here (Fig. 4). In contrast, the SDM predicted a relatively low occupancy probability (0.07) in Bahía La Herradura.

The mean water temperature (i.e., sea surface temperature) was the top predictor explaining the occupancy of *C. mutica* with a 44% contribution and 74% of the permuted importance (Table 2). The remaining predictors reached much lower contribution and permuted importance, often by one order of magnitude lower and < 10% (Table 2). The partial dependence plot revealed that the effect of the mean temperature was hump-shaped, with maximum occupancy probabilities around 11.3 °C, declining at lower and higher temperatures (Fig. 5).

Table 1. Surveys of the caprellid fauna in Central and South America (references included: ([13] Guerra-García and Thiel 2001; [2] Díaz et al. 2005; [3] Guerra-García et al. 2006; [1] Paz-Ríos et al. 2014; [5] Mauro and Serejo 2015; [8] Sánchez-Moyano et al. 2015; [6] Ros et al. 2016; [9] Alarcón-Ortega et al. 2017; [7] Nunez Velazquez et al. 2017; [4] Cunha et al. 2018; [10] Chunga-Llauce and Pacheco 2021; [12] Tapia-Ugaz et al. 2022; [11] Chunga-Llauce et al. 2023b). Note that only confirmed records on species-level were considered in the table.

Ocean	ATLANTIC										**Sum of Occurrences**	PACIFIC								**Sum of Occurrences**
Country	**Mexico [1]**	**Venezuela [2]**	**Colombia [3]**	**Brazil [4,5,6]**						**Argentina [7]**		**Mexico [8,9]**				**Peru [10,11,12]**			**Chile [13]**	
Latitude	**21°N**	**10°N**	**11°N**	**22°S**	**23°S**	**23°S**	**24°S**	**25°S**	**27°S**	**38°S**	**Atlantic**	**23°N**	**21°N**	**20°N**	**19°N**	**5°S**	**9°S**	**10°S**	**30°S**	**Pacific**
Survey Year	**2013**	**1980–2003**	**1986**	**2012**	**2008**	**2012**	**2009**	**2012**	**2012**	**2015**		**2008**	**2008**	**2002**	**2012–2016**	**2020**	**2019**	**2021**	**2000**	
Aciconula acanthosoma											**0**	x	x		x					**3**
Aciconula tridentata						x					**1**									**0**
Caprella californica											**0**						x			**1**
Caprella danilevskii		x	x		x				x		**3**									**0**
Caprella dilatata				x	x	x		x	x		**5**									**0**
Caprella equilibra		x		x	x	x		x	x	x	**7**		x			x	x	x	x	**5**
Caprella mendax											**0**	x			x					**2**
Caprella penantis		x	x							x	**3**					x		x		**2**
Caprella penantis f. gibbosa											**0**					x		x		**2**
Caprella pitu											**0**	x	x	x	x					**4**
Caprella scaura				x	x	x		x	x		**5**					x	x	x	x	**4**
Caprella suprapiscis											**0**				x					**1**
Caprella verrucosa											**0**						x		x	**2**
Caprellina longicollis											**0**								x	**1**
Deutella caribensis			x								**1**									**0**
Deutella incerta	x	x	x				x				**4**									**0**
Deutella margaritae	x	x									**2**									**0**
Deutella mayeri			x								**1**									**0**
Deutella venenosa											**0**							x	x	**2**
Hemiaegina minuta	x	x	x								**3**									**0**
Hemiproto wigleyi	x	x									**2**									**0**
Liropus guerragarciai							x				**1**									**0**
Liropus isabelensis											**0**	x	x		x					**3**
Mayerella redunca	x	x									**2**									**0**
Mayerella sittropiae							x				**1**									**0**
Metaprotella hummelincki	x										**1**									**0**
Paracaprella carballoi											**0**		x		x					**2**
Paracaprella digitimanus		x									**1**									**0**
Paracaprella dubiaski								x	x		**2**									**0**

Ocean	ATLANTIC										Sum of Occurrences	PACIFIC								Sum of Occurrences
Country	Mexico [1]	Venezuela [2]	Colombia [3]	Brazil [4,5,6]						Argentina [7]		Mexico [8,9]				Peru [10,11,12]			Chile [13]	
Latitude	21°N	10°N	11°N	22°S	23°S	23°S	24°S	25°S	27°S	38°S	Atlantic	23°N	21°N	20°N	19°N	5°S	9°S	10°S	30°S	Pacific
Survey Year	2013	1980–2003	1986	2012	2008	2012	2009	2012	2012	2015		2008	2008	2002	2012–2016	2020	2019	2021	2000	
Paracaprella isabelae											0	x			x					2
Paracaprella pusilla	x	x	x	x		x	x	x	x		8				x			x	x	3
Paracaprella tenuis	x				x						2									0
Pseudaeginella biscaynensis	x	x									2									0
Pseudaeginella colombiensis			x								1									0
Pseudaeginella montoucheti					x	x			x		3									0
Phtisica marina	x	x		x							3									0
Tritella chibcha			x								1									0
											25 species									16 species

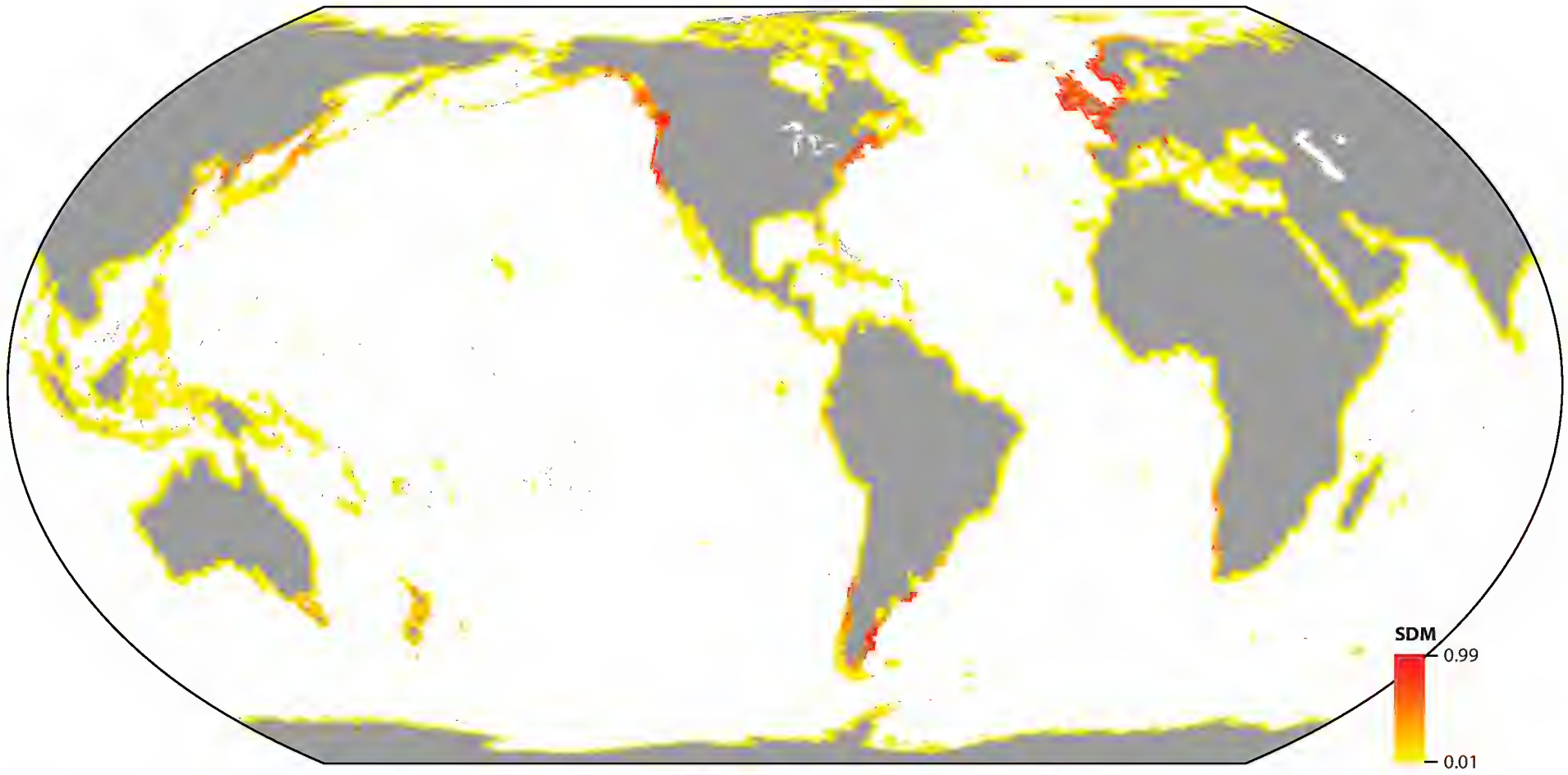

Figure 3. Probability of occupancy of *Caprella mutica* in coastal regions worldwide according to a calibrated SDM. Values closer to 1 (red) indicate higher occupancy probabilities, whereas values close to 0 (yellow) suggest lower occupancy probabilities. The SDM was calibrated at a 0.08° resolution, but is displayed here at a 1° resolution aggregation scale to improve visualization.

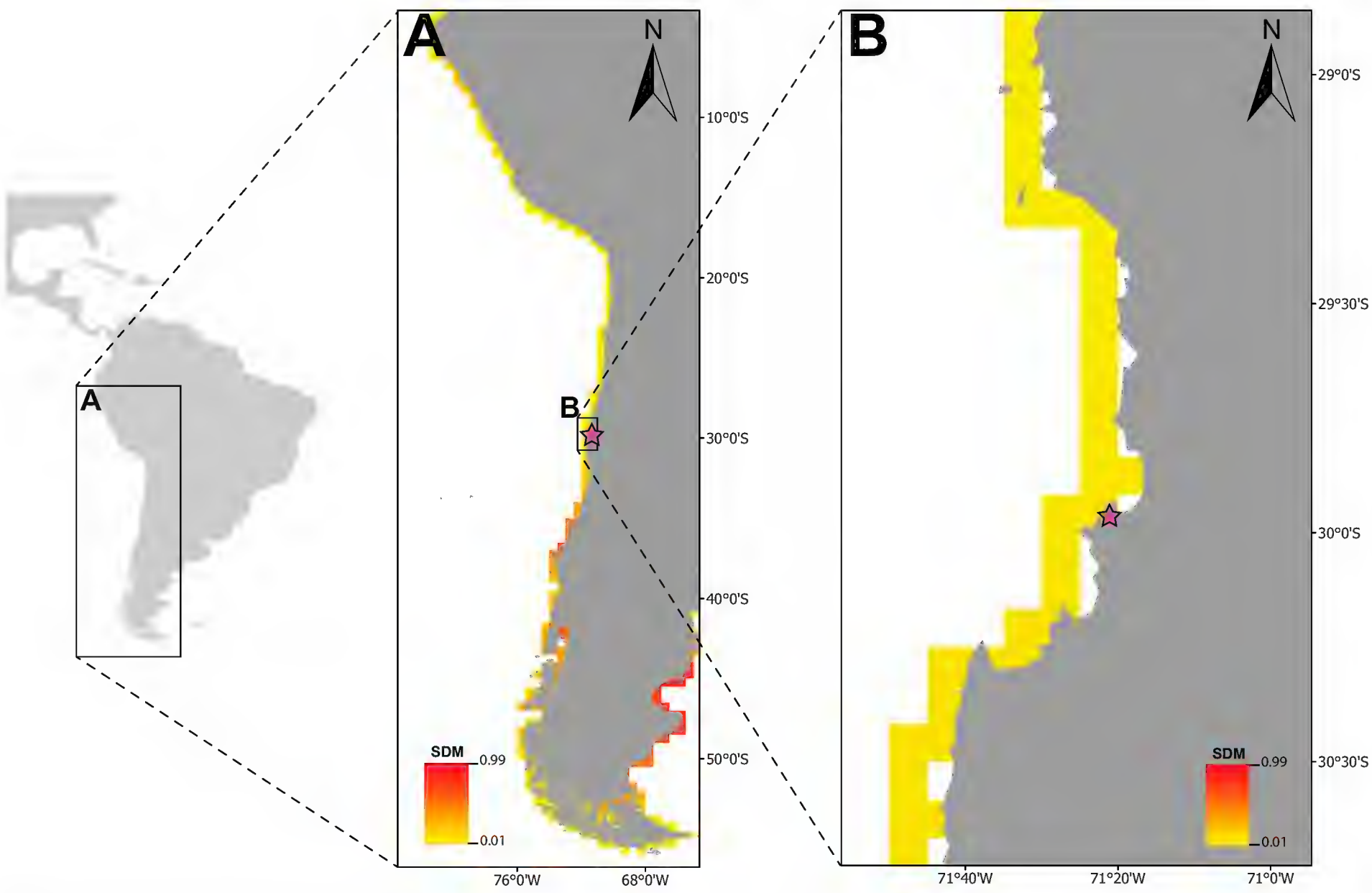

Figure 4. Probability of occupancy of *Caprella mutica* in **A** the Southeastern Pacific and **B** in Coquimbo, Chile according to a calibrated SDM. Values closer to 1 (red) indicate higher occupancy probabilities, whereas values close to 0 (yellow) suggest lower occupancy probabilities. The SDM was calibrated at a 0.08° resolution, but is displayed in **A** at a 0.5° resolution aggregation scale to improve visualization. Asterisks mark the location of Coquimbo in northern central Chile.

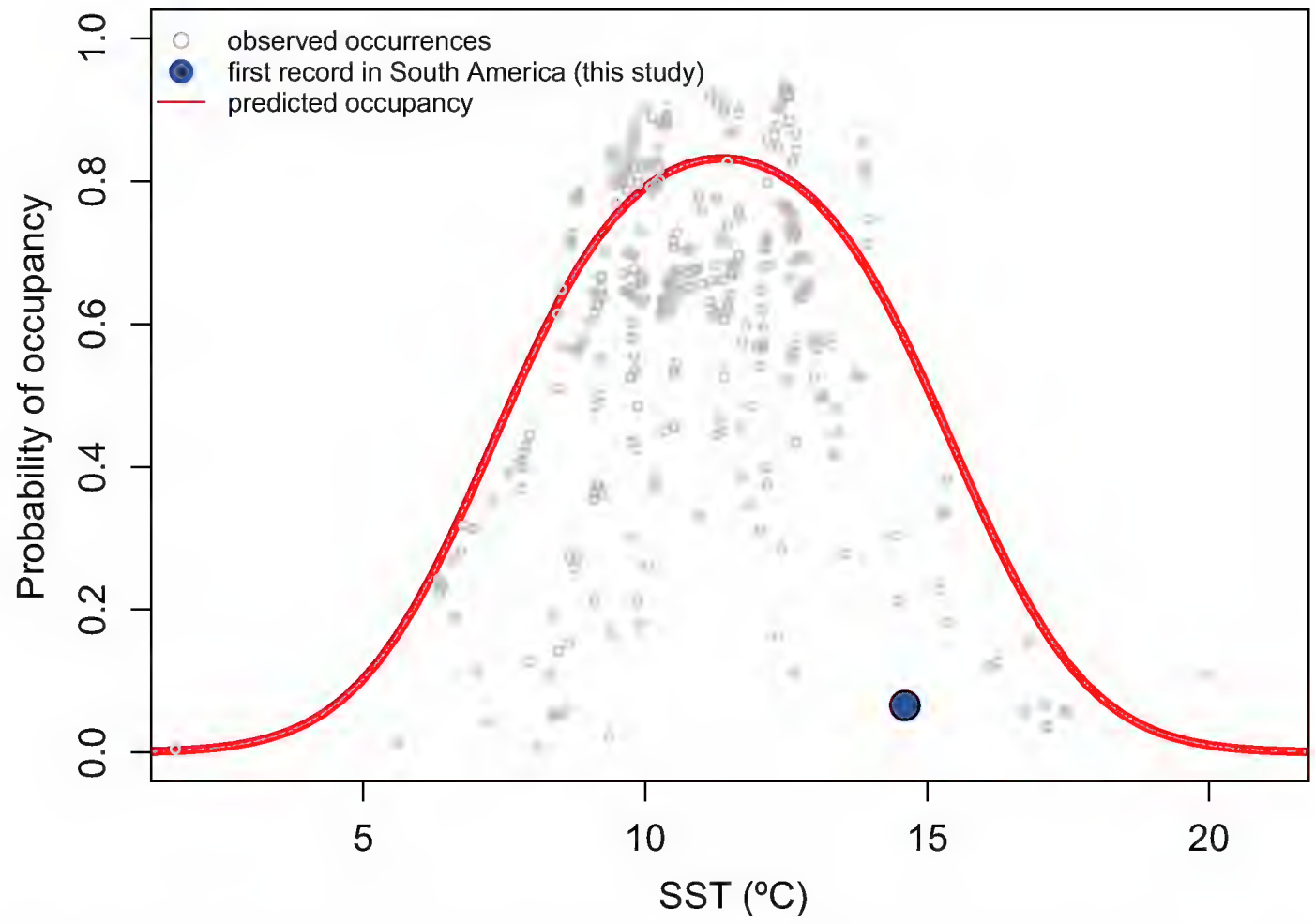

Figure 5. Functional relationships between occupancy probability and mean water temperature according to the species distribution model. Each empty dot represents the occupancy probability estimated for each global georeferenced occurrence. The red line shows the partial dependence plot of the isolated effect of mean water temperature on the occupancy probability. The blue dot indicates the new occurrence site in La Herradura Bay, Chile.

Table 2. Variance inflation factor (VIF) and relative importance of 11 oceanographic variables in an SDM of *C. mutica*. The mean and range of phytoplankton concentration were excluded from the analyses due to their high VIF (> 10).

Variable	VIF	% contribution	Permutation Importance
Temperature mean	4.4	44.3	73.5
Primary productivity mean	2.0	17.7	6.1
Chlorophyll mean	1.6	10.6	1.4
Salinity range	1.4	7.0	2.0
Temperature range	7.5	7.0	3.7
Salinity mean	7.3	5.7	2.6
Diffuse attenuation mean	10.0	2.7	3.2
Chlorophyll range	1.6	2.6	3.0
Silicate mean	8.0	1.3	2.0
Silicate range	3.0	0.7	0.9
Primary productivity range	3.0	0.4	1.5

Discussion

First record of *Caprella mutica* in South America

The current finding of *C. mutica* in Chile represents the first record of this caprellid in South America. Native to the north-east Pacific and introduced to the coasts of North America, Europe, New Zealand and South Africa, *C. mutica* seems to prefer cold-temperate waters (e.g. Arimoto 1976; Ashton et al. 2008b; Willis et al. 2009; Peters and Robinson 2017). Based on the known temperature tolerances of *C. mutica* and given its invasion history, Boos et al. (2011) predicted the species' potential to extend its range to

southern Pacific and Atlantic coasts of South America which is now corroborated by our recent finding.

The finding of several adult males and an ovigerous female in Coquimbo in 2022, and the collection of additional adult individuals in 2023 suggests the successful establishment of a population in Bahía La Herradura. However, the observed abundances were quite low compared to the known mass occurrences of *C. mutica* in other introduced ranges (e.g. Buschbaum and Gutow 2005; Peters and Robinson 2017). This could be due to (a) competition with other well-established local caprellid species along with (b) suboptimal environmental conditions for *C. mutica*, or (c) simply be the result of a very recent arrival of this invader in the region. Since *C. mutica* had previously never been observed in Coquimbo despite annual scans of the local caprellid fauna, it is indeed likely that this species has arrived relatively recently. Furthermore, the fact that *C. mutica* has not been reported from other regions in Central and South America, where extensive surveys of the caprellid fauna had been conducted by experts (see Table 1 and references therein), also suggests that this species has only recently arrived in South America. Most of these other studies have surveyed several sites within a country or ecoregion, and explicitly focused on the caprellid fauna (e.g. Díaz et al. 2005; Guerra-García et al. 2006; Paz-Ríos et al. 2014; Chunga-Llauce et al. 2023b), and thus the absence of the highly characteristic *C. mutica* in these surveys strongly suggests that it had not been present in those previous surveys. Since many of these surveys included taxonomical experts for the crustacean family Caprellidae who examined hundreds of specimens, it is considered very unlikely that *C. mutica* would have been overlooked. The population development of *C. mutica* in northern-central Chile must thus be monitored carefully, also with regards to any negative impacts on the local fauna such as the endemic *Deutella venenosa*.

Realized niche space of *Caprella mutica*

Overall, the predicted global occupancy probabilities reflected well the known native range of *C. mutica* as well as its occurrence in areas where it has been introduced (i.e. northern Europe and North America). The modelled predictions of our quantitative approach presented here are roughly in accordance with the "potential range" of *C. mutica* depicted by Boos et al. (2011). In direct comparison to the predicted probabilities in the northern hemisphere, the southern hemisphere seems to be less favorable for this caprellid species. The highest occupancy probabilities for *C. mutica* along the southeastern Pacific coast were observed around 32° and 42°S and were comparatively low in other areas such as Ecuador, Peru, as well as northern and southern Chile. Surprisingly, the SDM predicted only low occupancy probabilities for the Coquimbo Bay (0.07), well below other areas with a similar temperature, which is seemingly in contrast to the recent finding reported here. This new population might thus be living under near-suboptimal conditions that may prevent excessive population growth. A possible explanation could be that the original point of introduction of *C. mutica* to South America may have been located in central-south Chile with its large ports (i.e., San Antonio, Valparaíso and San Vicente) at 33° and 36°S, respectively, where predicted occupancy probabilities increased to up to 0.65. The species may, therefore, already have built undetected populations elsewhere that remain to be found. Further, the local population of *C. mutica* in Bahía La Herradura may be at its

physiological limit, reducing the probability of a northward expansion towards northern Chile and Peru. Nonetheless, also if the original point of introduction was indeed in Bahía La Herradura, a further southward expansion to areas where oceanographic conditions could be more favorable, seems likely.

Mean water temperature was the most important variable driving the environmental niche of *C. mutica*. The predicted thermal tolerance according to the SDM, however, is much lower compared to estimations based on ecophysiological experiments (Ashton et al. 2007; Hosono 2011). The median lethal temperature for adults was estimated at 28.3 ± 0.4 °C, while no mortalities occurred at 2 °C, even surviving below-zero temperatures (Ashton et al. 2007). Nevertheless, occupancy probabilities fell below 0.05 at temperatures lower than 5 °C or above 20 °C (Fig. 5). Interestingly, rearing experiments revealed that early stages of C. mutica reach maturity in the range of 10–20 °C, but not at 5 °C (Hosono 2011). All things considered, this suggests that the geographic spread of the species is not only driven by water temperature and it may be strongly co-dependent on the life stage of the animals.

Transport vectors and invasion scenarios along the southeast Pacific coast

The high densities of caprellid amphipods on aquaculture installations and especially on buoys indicate that aquaculture activities might contribute to the dispersal of caprellids along the Chilean and also the Peruvian coast (Thiel et al. 2003; Chunga-Llauce et al. 2023b). In fact, these buoys frequently become detached and are often found floating in coastal waters (Astudillo et al. 2009). The fouling assemblages previously identified on these lost aquaculture buoys contained all caprellid species currently known for the coasts of the SE Pacific (Astudillo et al. 2009). Now *C. mutica* is also found on these highly buoyant substrata, which likely will facilitate its future establishment and spread.

High densities and species richness of caprellids were also found on boat hulls in Peru (Chunga-Llauce et al. 2023b), indicating that small boats also might contribute to the transport of caprellids and other species along the SE Pacific coast. The recent finding of *Deutella venenosa*, a species that previously had only been reported from Coquimbo (30°S) in Chile, from aquaculture structures and boat hulls in Peru (Chunga-Llauce et al. 2023a), indicates that these substrata contribute to the dispersal of caprellids. Rafting dispersal on detached aquaculture structures is also supported by another recent finding of *D. venenosa* on a rope stranded at Ritoque Beach at 33°S (Rech et al. 2023), which could also be expected for *C. mutica* in the future.

Recent records of *Paracaprella pusilla* from Mexico, Costa Rica and Peru (Alarcón-Ortega et al. 2015; Alfaro-Montoya and Ramírez Alvarado 2018; Chunga-Llauce et al. 2022), which had earlier been confirmed at multiple sites near the Pacific entrance of the Panama canal (Ros et al. 2014), suggest another ongoing caprellid expansion along the East Pacific coasts. While most of these findings were made on suspended aquaculture structures, all authors consider transport in/on ships as a more likely cause for the recent appearance of *P. pusilla*.

Several other NIS have recently been reported along the Chilean coasts, including the sea anemones *Diadumene lineata* (Verrill, 1869) (Häussermann et al. 2015), *Metridium senile* (Linnaeus, 1761) (Molinet et al. 2023), and the tunicate *Asterocar-*

pa humilis (Heller, 1878) (Pinochet et al. 2017). In many of these cases, dispersal on ship hulls is considered most likely (Pinochet et al. 2023). For several seaweeds, aquaculture activities and intentional introductions are considered likely causes for recent introductions or range expansions along the Chilean coast (Camus et al. 2022; Jofré Madariaga et al. 2023). Many NIS thrive on floating structures (including aquaculture floats and ship hulls), which facilitates their dispersal and establishment in harbors (Leclerc et al. 2020). All this suggests that shipping activity might have led to the initial introduction of *C. mutica* to the coast of Coquimbo, and that abundant floating structures have then allowed the establishment of a local population.

Conclusions and outlook

The recent finding of *C. mutica* confirms the projection of Boos et al. (2011) who denoted some areas around the world, with South America among them, to be potentially sensitive for the arrival of this caprellid. The global spread of *C. mutica* seems to be ongoing, which is corroborated by recent records from previously unaffected global regions such as South Africa (Peters and Robinson 2017). As the large-scale oceanographic conditions appear suitable for *C. mutica* especially along the South American Pacific coasts and given the vectors and invasion history of other caprellid NIS, a further spread of this invader in South America seems to be inevitable. Therefore, *C. mutica* could now be considered to have become a true 'neocosmopolitan' (*sensu* Darling and Carlton 2018).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: JB, MT. Data curation: JB. Formal analysis: MMR, JB. Funding acquisition: MT. Investigation: JB. Resources: MT. Visualization: JB. Writing - original draft: MT, JB, MMR. Writing - review and editing: JB, MMR, MT.

Author ORCIDs

Jan Beermann https://orcid.org/0000-0001-5894-6817
Marcelo M. Rivadeneira https://orcid.org/0000-0002-1681-416X
Martin Thiel https://orcid.org/0000-0001-7535-3888

Data availability

All of the data that support the findings of this study are available in the main text

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